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Facultative myrmecophily in a highly endangered population of *Plebejus idas* (Linnaeus, 1761) in the northern Upper Rhine Valley (Lepidoptera, Lycaenidae)

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Abstract. Life history traits of the Idas Blue (*Plebejus idas* (Linnaeus, 1761)) were studied at two sites in the northern Upper Rhine valley in Baden-Württemberg (Germany). The species is monophagous on Broom (*Cytisus scoparius* (L.) Link) at these localities, as has been the case at numerous surrounding sites of former occurrence. Five species of formicine ants – *Formica pratensis* Retzius, 1783, *F. rufibarbis* Fabricius, 1793, *F. cunicularia* Latreille, 1798, *Lasius niger* (Linnaeus, 1758) and *L. psammophilus* Seifert, 1992 – have been found attending caterpillars and one pupa. Oviposition, including size of plants used and height above ground, was also studied. Based on the variety of ant partners and the apparent absence of ant-dependent oviposition, we conclude that the studied population exhibits the traits of facultative myrmecophily. In contrast, other Central European populations of *P. idas* hitherto studied are obligatorily myrmecophilous, usually showing associations with ants of the *Formica cinerea*-group. Thus, a fundamental intraspecific difference concerning the degree of myrmecophily has been demonstrated for the first time in a lycaenid species. Patterns of geographic variation of life histories in *P. idas* are discussed, though available information is scanty. The findings on caterpillar-ant associations in the Upper Rhine valley are highly relevant for conservation issues of the local population of *P. idas*, which is close to extinction. Shifts in the ant fauna and structure of broom patches are supposedly not very important factors in the species' regional decline. Nevertheless, protection measures for dry heathland such as soil disturbance may benefit ant density and thus *P. idas* on a local scale.

Introduction

Caterpillars (and sometimes pupae) of numerous butterfly species of the family Lycaenidae engage in close interactions with ants (Hymenoptera, Formicidae), a phenomenon termed myrmecophily (Fig. 1). This subject has been extensively reviewed by Fiedler (1991, 2006, 2021), Pierce et al. (2002) and Pierce and Dankowicz (2022a). Fiedler (1991) distinguished between facultative and obligatory relations between caterpillars and ants. In the latter case, larvae are dependent on the presence of workers of a certain ant species (or of few closely related species) while feeding on their host plant. Other traits are the assurance of the ants' presence by females when laying eggs (ant-dependent oviposition) and often a wider range of suitable larval host plants, as the importance of the particular ant partners takes precedence over that of diet (Pierce and Elgar 1985; Fiedler 1991; Pierce et al. 2002). In both obligatory and facultative myrmecophily, ants can access nutriments by means of specialized glands developed

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by the caterpillars (e.g. Pierce et al. 1987; Fiedler and Saam 1995), but it has increasingly been questioned in many cases whether an actual net benefit for ants exists (Pierce and Dankowicz 2022a, b). Caterpillars, in turn, are gaining at least partial protection from predators and parasites when tended by ants (e.g. Pierce and Easteal 1986; Hill et al. 2022). A particular case of obligatory associations are the parasitic species of the genus *Phengaris* Doherty living inside *Myrmica* Latreille ant colonies, as there is no symbiotic relationship developed in this case (e.g. Fiedler 1998; Hölldobler and Kwapich 2022). Apart from that, there are relatively few species of lycaenids in the Palearctic fauna that exhibit obligatory trophobiotic ant-associations. This trait is more common in tropical zoogeographic regions, particularly in the Australis (Eastwood and Fraser 1999; Eastwood et al. 2008). Among European non-parasitic lycaenids, only *Plebejus argus* (Linnaeus, 1758) and *Plebejus idas* (Linnaeus, 1761) show relationships with ants to be classified as obligatory myrmecophily (Fiedler 2021).

The Idas Blue (*P. idas*, Figs 5, 13, 14, 19), as presently delimited by most authors (e.g. Tshikolovets 2011), has a vast holarctic distribution with largely contiguous ranges in the Nearctic and the eastern Palearctic. In Europe, its distribution becomes increasingly patchy towards the West, with many isolated populations in the Iberian and Apennine Peninsulas (e.g. Lafranchis 2004). Nevertheless, *P. idas* can thrive in a wide variety of climatic conditions as populations range from southern Italy to the North Cape, occurring from planar to montane habitats (up to over 2000 m in the Alps). Accordingly, about 50 species of host plants from four families (Fabaceae, Elaeagnaceae, Cistaceae, Ericaceae) have been reported (Clarke 2022), with distinct regional variation (e.g. Henriksen and Kreutzer 1982; Weidemann 1995; Ulrich 2004; Bolz and Bräu 2013). Evolutionarily divergent populations with different habitat requirements should therefore be recognized and emphasized in the development of conservation programmes (see Thomas et al. 1999 for *P. argus*).

Figure 1. L_4 larva of *Plebejus idas* in association with three workers of *Formica pratensis* at Mörscher Hardt, Baden-Württemberg, Germany, 14.vii.2022. – Photograph by P. Schullerer.

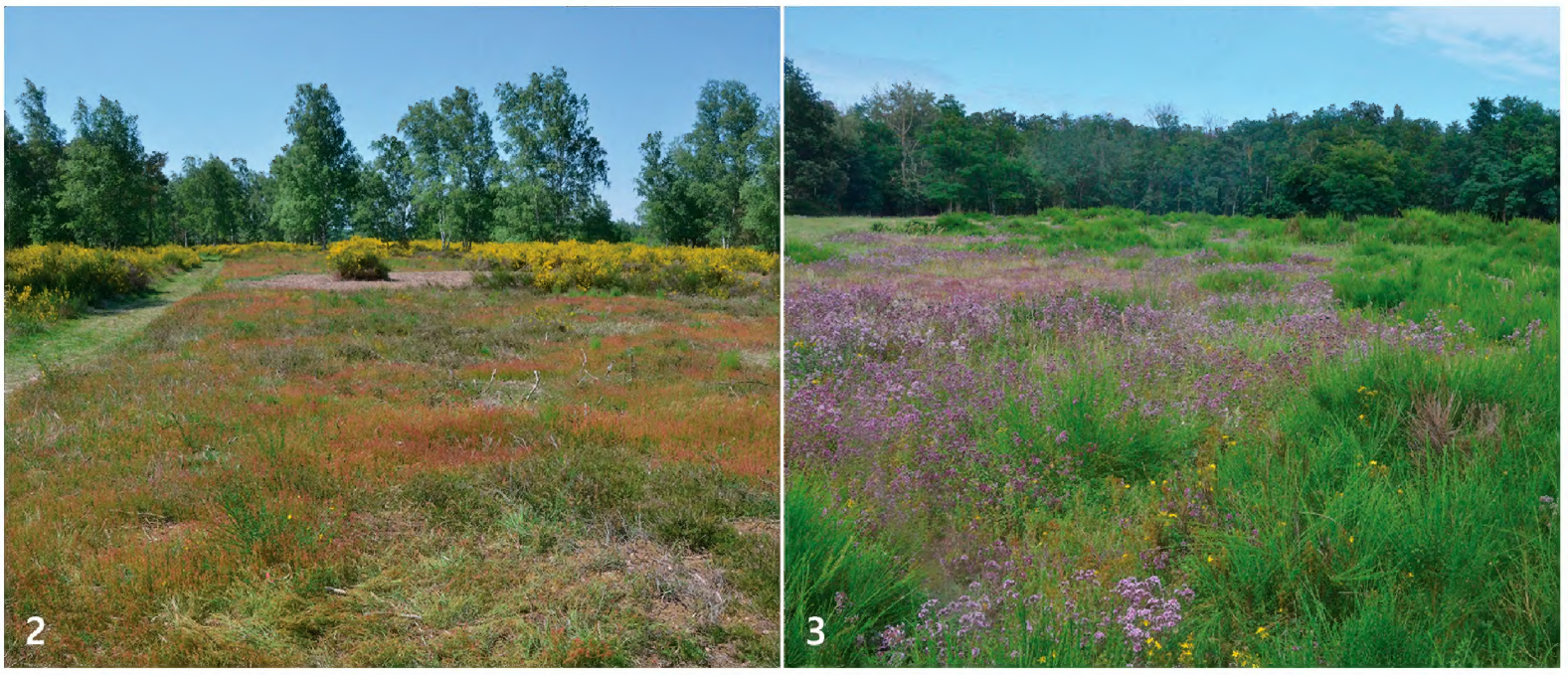
Plebejus idas shows a scattered distribution in Germany (Trusch et al. 2024) and is regarded as an endangered species (Reinhardt and Bolz 2012). Nonetheless, its conservation status varies widely among regions. Populations appear to be largely stable in northeastern Germany (Brandenburg: Gelbrecht et al. 2016) and, at least in anthropogenous habitats, in southern Bavaria (Bolz and Bräu 2013), even locally expanding in northern Switzerland (Jutzeler, in litt.). Conversely, declines have been precipitous in the North of the country (Schleswig-Holstein except North Frisian Islands: Kolligs 2021) and in the Southwest. In particular, the population in the northern Upper Rhine valley (in the state of Baden-Württemberg) is close to extinction, as a monitoring scheme by the species protection programme has demonstrated. Its life history differs from other populations in Germany in that Broom (*Cytisus scoparius* (L.) Link), a shrubby legume, serves as the only larval host plant of both generations. In Bavaria, a wide variety of herbaceous Fabaceae is used at most localities (Bolz and Bräu 2013). Information about host plants in northern/northeastern Germany is scanty, however, Common Heather (*Calluna vulgaris* (L.) Hull, Ericaceae) has been reported for Schleswig-Holstein (Kolligs, in litt.) and Brandenburg (Miethke 2011), locally in combination with *C. scoparius* (Gelbrecht et al. 2016).

Concerning myrmecophily, evidence for obligatory ant associations *sensu* Fiedler (1991) has been presented for populations of *P. idas* in Switzerland (Jutzeler 1989, 1990). Almost all of the substantial literature for Bavaria and the Suisse lowlands indicates three closely related species of the *Formica cinerea*-group as the only ant partners (Schweizerischer Bund für Naturschutz 1987; Jutzeler 1989, 1990; Bolz 1998; Pfeuffer 2003, 2005). Pupation occurs in close proximity to the nest entrances of those ants (Malicky 1961; Pfeuffer 1998) and even within the nest galleries (Thomann 1901), as in *P. argus* (e.g. Pontin 1990; Güsten et al. 2019). There is also evidence for peaceful coexistence of adults with their ant partners (Pfeuffer 1998). Information provided by Kolligs (in litt.) for northern Germany likewise hints at *Formica* (*Serviformica*) *cinerea* Mayr, 1853 as an ant species associated with *P. idas* caterpillars on common heather. In contrast, there are records of species both of the genera *Formica* Linnaeus and *Lasius* Fabricius (the latter documented by one photograph) as ant symbionts on *C. scoparius* in the Upper Rhine valley of Baden-Württemberg (Ebert and Rennwald 1991). This observation questions obligatory myrmecophily of *P. idas* in the region, which led us to attempt a detailed investigation of the life history of this highly endangered population.

Methods

Field studies were undertaken at two locations in Baden-Württemberg presently still harbouring remnant populations of *Plebejus idas*. The southern study site was located in the nature reserve Stollhofener Platte, Rheinmünster (48°45'40"N, 08°04'20"E, Fig. 2), while the northern study site constitutes a decommissioned army firing range in the Mörscher Hardt (forest) at Rheinstetten (48°56'15"N, 08°21'10"E, Fig. 3). The distance between the two sites is about 30 km. At a third locality (Malsch, disused gravel pit at parcel Luderbusch: 48°54'45"N, 08°19'50"E), about 3 km from the northern site, occurrence of *P. idas* had last been reported in 2019, but the species could not be found again during the course of the study. The species protection programme of the state of Baden-Württemberg has been monitoring *P. idas* at these sites since the 1990s, as well as at about 20 other sites still populated back then.

We observed oviposition in the second generation on 10.viii.2021 at Mörscher Hardt and on 21.viii.2021 at Stollhofener Platte. Both sites were visited on 14.vi.2023 in order to record



Figures 2, 3. Habitat of *Plebejus idas* in the northern Upper Rhine Valley, Baden-Württemberg, Germany: **2.** Stollhofener Platte nature reserve, 9.v.2022; **2.** Mörscher Hardt, 10.viii.2021. – Photographs by R. Güsten.

oviposition of the first generation. A search for caterpillars was undertaken on 09.v.2022 and 21.vii.2022 (Stollhofener Platte) and on 16.v.2022 and 14.vii.2022 (Mörscher Hardt), thus covering both generations at both sites. An additional search was carried out on 12.vii.2023 at both sites. For every caterpillar located, it was attempted to procure a sample (three specimens if possible) of the accompanying ants.

In order to elucidate whether broom shrubs of a certain size are preferred for larval development, or certain areas on the plants, the height above ground was recorded for the discovered larvae as well as for the eggs laid. Also, the total height of the respective host plants was documented. Eggs or eggshells discerned on broom during field work were noted, but a diligent search was not undertaken. Eggs are much more easily found on small plants than on large ones, thus including those data in the comparison would lead to skewed results.

To get an idea of potentially available ant partners, a non-quantitative and non-exhaustive survey of the ant fauna on broom, as well as in and around the broom patches at both sites was undertaken by seeking foraging workers and nests. Arboricolous and exclusively soil-dwelling ant species were thus not sampled, as they are extremely unlikely to act as symbionts of lycaenids.

Results

Caterpillar-ant associations

A total of 16 caterpillars of *Plebejus idas* were located on broom shrubs after intense searching in May (first generation) and July (second generation). Eight specimens each were found at the two study sites, with nine pertaining to the first and seven to the second generation (Table 1). All larvae were green with a darker greenish dorsal stripe and some dorsal and lateral white, but no black markings (Figs 1, 6–10, 15, 20). Most were in their last (fourth, see Powell 1917; Lafranchis et al. 2015) instar. About six caterpillars could be assigned to earlier instars (Table 2). Only two of those were distinctly smaller than the others and most probably still before moult to the third instar (Fig. 6). For one of the smaller larvae no sample of accompanying ants could be obtained. One *Lasius* sp. worker attending the larva escaped upon slight disturbance. This contrasted to the

Table 1. Caterpillar-ant-associations recorded for *Plebejus idas* in 2022 and 2023. Gen. = Generation.

Locality		*Formica pratensis*	*Formica rufibarbis*	*Formica cunicularia*	*Lasius psammophilus*	∑
Stollhofener Platte	1. Gen.		1		6	9
	2. Gen.	1 (pupa)			1	
Mörscher Hardt	1. Gen.	2				8
	2. Gen.	6		[1]†		
∑		**9**	**1**		**7**	**17**

†single worker of *F. cunicularia* together with several *F. pratensis*, not counted towards totals

behaviour of all ants associated with larger larvae, which needed much stronger intervention to abandon their symbiotic partners. Also, at least two (and up to six) ant workers were initially seen with all larvae except the mentioned smallest one.

At Mörscher Hardt, all accompanying ants represented the species *Formica* (s. str.) *pratensis* Retzius, 1783 (Figs 1, 15, 18), apart from one worker of *Formica* (*Serviformica*) *cunicularia* Latreille, 1798 sitting on a caterpillar otherwise associated with several *F. pratensis* workers. At Stollhofener Platte, ant partners recorded were *Lasius* (s. str.) *psammophilus* Seifert, 1992 (likely 7 caterpillars, Figs 7, 10) and *Formica* (*Serviformica*) *rufibarbis* Fabricius, 1793 (1 caterpillar, Fig. 9). However, a pupa was also found on a narrow but fairly tall broom shrub (Fig. 4, Table 1) at this site, accompanied by workers of *F. pratensis* (Fig. 8). Given that the pupa was attached at a height of 85 cm, the larva had certainly not made any effort to descend to the base of the plant or to the leaf litter for pupation. The pupa was collected in order to ascertain determination, and a male of *P. idas* eclosed 13 days later.

Two larvae at Mörscher Hardt, and three larvae at Stollhofener Platte were found concurrently on the same broom shrub. In the latter case, the rather small plant was largely defoliated, and the caterpillars appeared to feed on some remaining flowers (Fig. 7).

Only one larva of the second generation at Mörscher Hardt was found in 2023, while all other records originated from 2022 (Table 2). Overall population density was extremely low in 2023, and just one or two females of the first generation were seen at each locality.

While *P. idas* wasn't found at Malsch during our field study, it was possible to determine *Lasius* (s. str.) *niger* (Linnaeus, 1758) as the ant species accompanying two caterpillars at this site by means of earlier high-quality photographs (Fig. 20) taken on a joint field trip by Matthias Sanetra and Arik Siegel.

Ant fauna at study sites

In addition to the three species accompanying the early stages of *P. idas* at Stollhofener Platte (*L. psammophilus*, *F. rufibarbis*, *F. pratensis*), two other ant species of the subfamily Formicinae were commonly recorded at the site: *Formica* (*Raptiformica*) *sanguinea* Latreille, 1798 and *Camponotus ligniperda* (Latreille, 1802). The latter regularly attended groups of the treehopper *Gargara genistae* (Fabricius, 1775) (Hemiptera, Membracidae), and sometimes other Auchenorrhyncha, on broom, much as the other above-mentioned formicines did (Fig. 15). In contrast, *F. sanguinea* was not seen visiting honeydew-producing insects on broom, even though trophobiosis has been recorded in this species (Seifert 2018). Some species of the subfamily Myrmicinae were also present at the site (e.g. *Myrmica schencki* Viereck, 1903), but only *Tetramorium caespitum* (Linnaeus, 1758) showed some association with broom as it often built nests at the base of small plants. The species, however, was not seen foraging higher up in the bushes than around 10 cm above ground.

Figures 4–12. *Plebejus idas* at Stollhofener Platte, Baden-Württemberg, Germany. **4.** Tall broom shrub with pupa (Fig. 8) at height of 85 cm (arrow), 21.vii.2022; **5.** Male nectaring on common heather, 21.viii.2021; **6.** L_2 larva, initially seen with worker of *Lasius* cf. *psammophilus*, 9.v.2022; **7.** Two L_4 larvae on broom flower, attended by *L. psammophilus*, 9.v.2022; **8.** Pupa attended by *Formica pratensis*, 21.vii.2022; **9.** L_4 larva with *F. rufibarbis*, 9.v.2022; **10.** L_4 larva with *L. psammophilus*, 9.v.2022; **11.** Small broom on sandy path (Fig. 12) with egg-laying female (arrow) near its base, 21.viii.2021; **12.** Cleared patch adjacent to sandy path harbouring eggs and larvae, 9.v.2022. – Photographs by R. Güsten and M. Sanetra (5, 11).

Table 2. Details of individual observations of caterpillars of *Plebejus idas*. Height *L* = Height of larvae or pupae on host plant in cm when detected; Height *P* = Total plant height in cm. Height *P* not given if larva on same plant as previously listed larva.

Locality	Date	Stage	Height *L*	Height *P*	Ant species
Stollhofener Platte (nature reserve)	9.v.2022	L4	20	35	*Lasius psammophilus*
	9.v.2022	L4	35	55	*Formica rufibarbis*
	9.v.2022	L2	15	45	*Lasius* cf. *psammophilus*
	9.v.2022	L4	30	55	*Lasius psammophilus*
	9.v.2022	L4	30		*Lasius psammophilus*
	9.v.2022	L3	50		*Lasius psammophilus*
	9.v.2022	L4	25	40	*Lasius psammophilus*
	21.vii.2022	Pupa	85	150	*Formica pratensis*
	21.vii.2022	L4	55	90	*Lasius psammophilus*
Mörscher Hardt (former firing range)	16.v.2022	L2	75	140	*Formica pratensis*
	16.v.2022	L4	60	100	*Formica pratensis*
	14.vii.2022	L4	90	165	*Formica pratensis*†
	14.vii.2022	L4	85	120	*Formica pratensis*
	14.vii.2022	L4	85		*Formica pratensis*
	14.vii.2022	L3	85	130	*Formica pratensis*
	14.vii.2022	L3	70	120	*Formica pratensis*
	12.vii.2023	L3	75	115	*Formica pratensis*

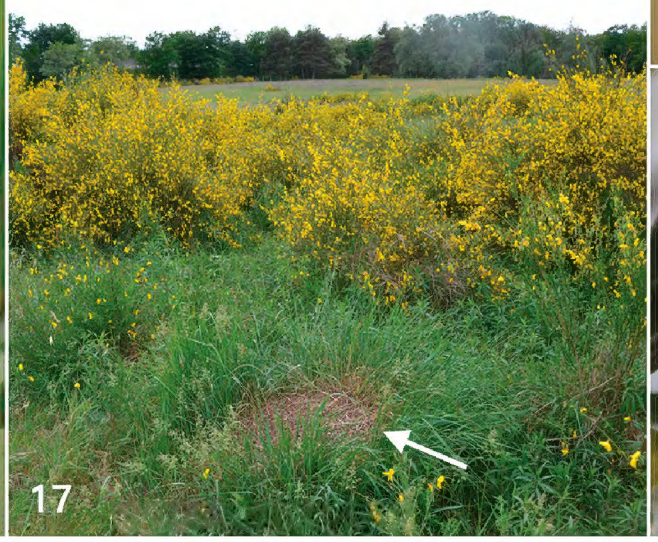
†additionally one worker of *F. cunicularia*

At Mörscher Hardt, the two ant species attending *P. idas* caterpillars (*F. pratensis*, *F. cunicularia*) were the most common formicines in and around the broom patches. *Formica rufibarbis* also occurred but was clearly less prevalent than its close relative *F. cunicularia*. One worker of *Formica* (*Serviformica*) *fusca* Linnaeus, 1758 was collected, a species usually inhabiting woodland. Colonies of *Lasius* spp. were rather local, and all those checked pertained to *L. niger*, while *L. psammophilus* was not recorded. From other subfamilies, *T. caespitum*, *M. schencki* and *Myrmica sabuleti* Meinert, 1861 (Myrmicinae) were present, as was *Tapinoma erraticum* (Latreille, 1798) (Dolichoderinae).

Habitat of early stages

No preference could be detected for caterpillars with regard to particularly high or low feeding or resting places on their host plants (Table 2). The measurements for height above ground varied between 35 and 165 cm (mean = 55.31, SD = 25.46, n = 16). Also, we could not find any relation for the preference of small (Fig. 11) versus tall plants (Figs 4, 17) as microhabitat of the caterpillars (mean = 93.08, SD = 41.26, n = 13). Furthermore, it appeared that the distribution of caterpillars on broom shrubs had no obvious pattern whether it was first- or second-generation offspring.

Observations of egg-laying females of *P. idas* could be achieved in the field for the second generation in August 2021 at both study sites. In total, 23 oviposition events involving 12 females were recorded. In 2023, population density of the first generation was far too small to get any results on oviposition. All eggs were laid on broom. This corresponds with all reports by other observers in the Upper Rhine valley over many years (particularly E. Rennwald, pers. comm.), even though other plant species known as host plants of *P. idas* do occur. At the two study sites, these are mainly common heather at Stollhofener Platte (Fig. 5) and Bird's-foot Trefoil (*Lotus corniculatus* L.) at Mörscher Hardt.



Figures 13–18. *Plebejus idas* at Mörscher Hardt, Baden-Württemberg, Germany. **13.** Female, 10.viii.2021; **14.** Male, 10.viii.2021; **15.** L_4 larva attended by *Formica pratensis* together with an adult treehopper (*Gargara genistae*, arrow), 14.vii.2022; **16.** Egg (arrow) on lignified broom sprout at height of 80 cm, 10.viii.2021; **17.** Large *F. pratensis* nest (arrow) in front of broom shrubs harbouring larvae, 16.v.2022; **18.** L_3 larva attended by *F. pratensis* on the underside of a leaf with its feeding mark, 12.vii.2023. – Photographs by R. Güsten and P. Schullerer (15).

Eggs were placed singly on sparsely distributed shrubs or at the margin of closed patches of broom rather than inside those patches. Nevertheless, sometimes a female would lay more than one egg (2-3) on the same plant. Woody branches close to side shoots (Fig. 16) or the axils of the shoots themselves were mostly used as oviposition sites. Oviposition on terminal, unlignified shoots was rarely observed. It appeared that in certain locations with much open sandy soil, depositing the eggs on smaller broom specimens was preferred, but oviposition in tall bushes at larger height also occurred. Overall, the height above ground for the recorded oviposition sites was quite variable, ranging from 10 to 140 cm (mean = 62.17, SD = 35.28, n = 23). We did not observe behavioural traits suggesting ant-dependent oviposition and in general, oviposition occurred rather quickly. Only on one occasion might a female have been aroused (bending the abdomen and showing oviposition behaviour) by the presence of *F. pratensis* ants walking about on a branch in proximity.

Discussion

Myrmecophily in the studied population

Plebejus idas has until now been classified as an obligatorily myrmecophilous lycaenid (Jutzeler 1989, 1990; Fiedler 2006; Bolz and Bräu 2013). The main traits of this type of interaction are dependence on one (or few closely related) species of ants, and ant-dependent oviposition. Ant attendance of pupae, often within ant nests, and peaceful interactions with adult butterflies have also been observed in *P. idas* (Thomann 1901; Malicky 1961; Pfeuffer 1998). In contrast to other studies, we found an array of attendant ant species in the investigated population of *P. idas*, although the five species demonstrated here belong to the same subfamily Formicinae. However, species of the genera *Formica* and *Lasius* are phylogenetically quite distant within the subfamily (typically classified in tribes Formicini and Lasiini, respectively, e.g. Ward et al. 2016). Also, while the subgenera *Formica* s. str. (socially parasitic) and *Serviformica* Forel (independent colony foundation) are traditionally classified within a very widely defined genus *Formica*, these taxa have diverged early in their phylogenetic history (e.g. Romiguier et al. 2018). Thus, *P. idas* in the northern Upper Rhine valley is clearly not in line with the situation found in well-known obligatory myrmecophiles, including other populations of *P. idas*. If more caterpillars could be observed at the two sites, it is quite possible that additional associated ant species would be found (particularly *Camponotus ligniperda*), maybe also non-formicine ones (e.g. *Tetramorium caespitum*). Essentially, the ant partners recorded at the two sites reflect the dominance patterns within the respective biotopes, as is typical for facultative myrmecophiles (Fiedler 2021).

The observations in this study also do not point towards ant-dependent oviposition, as eggs were deposited quite quickly without careful inspection of the substrate by the females and typically without ants being present, contrary to reports for obligatorily myrmecophilous populations of *P. idas* (Jutzeler 1989; Pfeuffer 1998). One would assume that assuring the presence of particular ants by the females is time-consuming and would include numerous unsuccessful attempts (as also observed in *Plebejus argus*, see Güsten et al. 2019). Monophagy of the investigated population (on *Cytisus scoparius*) is likewise untypical in obligatory myrmecophily (see Fiedler 1991).

It can therefore be concluded that the population of *P. idas* in the Upper Rhine valley is facultatively myrmecophilous, in contrast to all other populations of the species investigated thus far. As such profound intraspecific variation in relation to this important life history trait is an unusual finding, alternative explanations for the observed deviation need to be discussed:

(a) The classification of *P. idas* populations earlier investigated as obligatorily myrmecophilous has been erroneous.
(b) The situation presently observed in the Upper Rhine Valley is artificial, brought about by the local disappearance of obligatory ant partners.
(c) The populations in question are not truly conspecific.

Explanation (a). A large range of observations indicate confidently that only three closely related *Formica* (*Serviformica*) species of the *Formica cinerea*-group are suitable as ant symbionts of *P. idas* in Bavaria and at lower elevations in Switzerland (Jutzeler 1989, 1990; Bolz and Bräu 2013). In discordance to that, only Bolz and Bräu (2013) assert *Formica rufibarbis* and *F. fusca*

Figures 19, 20. *Plebejus idas* at Malsch, Baden-Württemberg, Germany (last record there 29.vii.2019). **19.** Copula, 8.viii.2013; **20.** L_4 larva with a worker of *Lasius niger* taking in fluid from the caterpillar's dorsal nectar organ, 13.vii.2015. – Photographs by T. Bamann (19) and A. Siegel (20).

(both from other species groups within the subgenus *Serviformica*) as associated with *P. idas* larvae in few cases. In Switzerland, quite convincing evidence for ant-dependent oviposition has been provided (Jutzeler 1989, 1990), although methods to conclusively prove this trait in Lycaenidae have yet to be developed (for an approach under laboratory conditions see Trager et al. 2013). The cited works also indicate a large range of host plants from three families (Fabaceae, Elaeagnaceae and Cistaceae) as is typical for obligatory myrmecophiles (Fiedler 1991).

Explanation (b). There is no known example of obligatorily myrmecophilous lycaenids being able to adapt to different ant species if their original hosts disappear. Their caterpillars are often attractive to other ants when reared in captivity (e.g. Bink 1992; Jutzeler et al. 2003), yet stable associations with deviating ant partners are extremely rare under natural conditions. The most manifest cases were documented for the Australian lycaenid *Jalmenus evagoras* (Donovan, 1805), when population outbreaks apparently led to a relative shortage of host plants harbouring their usual ant partners of the genus *Iridomyrmex* Mayr (Pierce and Nash 1999; Eastwood and Fraser 1999). Earlier descriptions and photographic records of current and former habitats of *P. idas* in the northern Upper Rhine Valley (e.g. Ebert and Rennwald 1991) do not indicate a fundamental change in vegetation cover. It seems unlikely that the herb layer in these biotopes was formerly so sparse that species of the *F. cinerea*-group abounded there. If the assignment of northern French populations of *P. idas* to the same ecotype is valid (see below), explanation (b) is automatically disproved, as northern France, except very locally in the east, is not within the range of any species of the *F. cinerea*-group (Blatrix et al. 2013; Galkowski 2024).

Explanation (c). There is by far not enough information on life history traits of the many regional variants of *P. idas* to presently consider a split of the species on this basis. As for *Phengaris alcon* (Denis & Schiffermüller, 1775) (Lycaenidae, e.g. Lucek et al. 2024), DNA-analyses might be used in the future to elucidate phylogenetic relationships among *P. idas* populations. To consider a

taxonomic split, it would have to be demonstrated that different life histories correspond to monophyletic entities. However, a shift in the nature of ant-lycaenid-interactions could well have occurred multiple times within the species, representing a geographic mosaic of coevolution (Thompson 2005). In parasitic *Phengaris* butterflies, local adaptations to host ant species can be interpreted in this way (Tartally et al. 2019). The geographic mosaic theory of coevolution comprises the idea that a species may adapt differently in separate regions regarding its interactions with other species (for further examples involving Lepidoptera see Singer and McBride 2012; Thompson et al. 2013).

Ecotypes of *P. idas* within Europe

We propose to define ecotypes of *P. idas* according to type of myrmecophily, host-plant usage and habitat structure. For the population of the northern Upper Rhine Valley we designate a broom ecotype (see also Weidemann 1995), which displays facultative myrmecophily and uses shrubby legumes as larval host plants. Supposedly, *P. idas* exhibits largely the same life history across the adjacent northern half of France. In Brittany, oviposition takes place on Gorse (*Ulex minor* Roth, *U. europaeus* L.) (Powell 1917; Maillard 2014, 2017), shrubs closely related to Broom (*Cytisus scoparius*). In the vicinity of host plants, large ant mounds (probably *F. pratensis*) but also small brown ants (probably *Lasius* sp.) were reported by Powell (1917). There is also a record of caterpillars on *C. scoparius* growing in a nest of *F. pratensis* (Maillard 2014), and one male was seen emerging from a *F. pratensis* nest (Perrein 2012). Similar life habits appear likely for Normandy (Bink 1992) and Lorraine (eggs on *C. scoparius*: Strätling 2009). All larvae described from Brittany were green as in Baden-Württemberg, though markings seemed to be more sombre.

The river gravel ecotype is obligatorily associated with ants of the *F. cinerea*-group (e.g. Jutzeler 1989, 1990; Bolz and Bräu 2013). It uses both numerous species of herbaceous Fabaceae and Sea Buckthorn (*Hippophae rhamnoides* L., Elaeagnaceae) as host plants, sometimes even simultaneously in the same population (Thomann 1901; Jutzeler 1989; Bolz and Bräu 2013). It corresponds to the sea-buckthorn-type of Weidemann (1995). In accordance with the rather specialized ecological requirements of its ant associates, this ecotype lives in alpine riverbeds (e.g. Pfeuffer 2003) and anthropogenic secondary habitats with very little vegetation, such as industrial areas and gravel pits (Schwibinger and Bräu 2001). It can occur in other environments very poor in vegetation (coastal dunes: Gourvil and Sannier 2022). Its caterpillars are very variable, even within populations, from green (dorsal stripe usually blackish) to mostly brownish or reddish, with intermediates.

There probably exists an alpine ecotype of *P. idas* at high elevations in the Swiss Alps, investigated by Jutzeler (1989). These populations appear to be monophagous on *Helianthemum* spp. (Cistaceae) and may obligatorily depend on ants of the subgenus *Formica* (*Coptoformica*) Müller. However, weak interactions of caterpillars with species of *Formica* s. str. and *Formica* (*Serviformica*) were also observed in a few instances.

Since further studies on caterpillar-ant relationships in *P. idas* are lacking, we cannot delineate additional ecotypes in Europe. Populations of *P. idas* occurring in heathland, where feeding on common heather is reported, are known from different regions across Germany (Reinhardt et al. 2007; Bolz and Bräu 2013; Gelbrecht et al. 2016; Kolligs 2021), termed *Calluna*-type by Weidemann (1995). However, it seems doubtful to characterize ecotypes in this species on host plant usage alone, considering the fundamental importance of different types of myrmecophily. There is also a lot of regional variation as regards larval host plants. In Scandinavia, for instance, herbaceous Fabaceae are described as the dominant host plants, but broom and common heather are also mentioned (Henriksen

and Kreutzer 1982; Bink 1992). One or few species of shrubby legumes serve as host plants of *P. idas* and its close relative *Plebejus bellieri* (Oberthür, 1910) in different parts of southern Europe (Jutzeler et al. 2003; Jutzeler and Leigheb 2004; Kolev 2005; Muñoz Sariot 2011), hence there could be a link to the broom ecotype. Nonetheless, there is no reliable information on the nature of myrmecophily in these regions, thus ecological networks have yet to be elucidated.

Conservation

The population investigated here has historically been much larger and was recorded from the northern Upper Rhine Valley in the German states of Rhineland-Palatinate and Baden-Württemberg, and in northern Alsace (France). In Rhineland-Palatinate it went extinct shortly after 1980 (Haag et al. 2007). The steady decline in Baden-Württemberg has been documented by monitoring through the state's species protection programme, which indicated a loss of about half of the sites between 1995 and 2009. Today there are only two known localities still inhabited by *P. idas*, thus the species is close to extinction in Baden-Württemberg. It is nevertheless possible that a few remnants still persist in northern Alsace. Given the adaptive divergence of *P. idas* in the Upper Rhine valley, the population should be considered an evolutionarily significant unit with high conservation value (sensu Fraser and Bernatchez 2001).

In the Upper Rhine Valley, the preservation of heathland with broom (and of interspersed nutrient-poor grassland on sand) constitutes an increasing struggle for nature protection management. This is due to ever rising nitrogen input, in these habitats largely through atmospheric deposition (e.g. Phoenix et al. 2012; Bähring et al. 2017), exacerbated by a particular high neophyte pressure of Canada Goldenrod (*Solidago canadensis* L.), American Black Cherry (*Prunus serotina* Ehrh.), Tree of Heaven (*Ailanthus altissima* (Mill.) Swingle) and others. An increase of ground cover by low vegetation occurs at some sites, and this likely reduces ant density in broom heathland. Reversing this trend may henceforth require soil disturbance by choppering or sod-cutting (e.g. Niemeyer et al. 2007; Pedley et al. 2013; Walmsley et al. 2021). Within a habitat a mosaic of rotating plots of soil disturbance is recommended, as ant colonies might get impaired initially. Even so, it is difficult to ascertain whether *P. idas* has actually been negatively affected by changes in low vegetation. Comparison of the two remaining sites of occurrence seems to indicate that enhanced ground cover reduces the abundance of *Lasius psammophilus* and *Formica rufibarbis*, but not *F. pratensis*. The southern site, where regular high-intensity mowing in patches (but without soil disturbance) is undertaken (Fig. 12), exhibits less ground cover than the northern site, which is grazed by goats.

The reasons for the extraordinarily rapid range contraction of *P. idas* in the Upper Rhine valley are therefore far from being understood. These unknown factors obviously affect other populations of the broom ecotype as well (Dardenne et al. 2008; Perrein 2012; Maillard 2017), but not those of the river gravel ecotype. Ebert and Rennwald (1991) regularly detected pre-imaginal stages on smaller broom shrubs, with little surrounding vegetation, which have become rarer in the past decades. However, the present study has demonstrated that larvae can be found in the upper half of large shrubs, where *Formica pratensis* (and potentially *Camponotus ligniperda*) are available as ant partners, to some extent also *F. rufibarbis* (and probably *F. cunicularia*). Only *L. psammophilus* is largely limited to attending caterpillars positioned at lower heights but can ascend at least to 55 cm (Table 2). The importance of particularly small host plants for *P. idas* is thus lower than previously thought, certainly not accounting for the extent of the species' decline in the area. Also, the current structure of broom patches is by itself an insufficient explanation. The associated ants

are thermophilous species and will no longer occur when a closed shrub cover is developed. As the presence of ants reduces larval mortality (e.g. Pierce et al. 1987; Hill et al. 2022), the interior of dense scrubland can hardly be suitable for the development of *P. idas*. While an increase of shrub cover has certainly occurred at many sites previously occupied by the species, fringes of broom patches should presently still provide reasonable habitat. A belt of well-spaced plants of different sizes persists at least in some sections at most former localities.

Conclusions

In Central and Western Europe *Plebejus idas* displays a number of ecotypes, which may differ in the nature of their interactions with ants, in addition to host plants and habitat structure. Populations of the broom ecotype investigated here (northern Upper Rhine valley, also occurring in northern France) are facultatively myrmecophilous, while populations of the river gravel ecotype in Bavaria and Switzerland exhibit the traits of obligatory myrmecophily. Such fundamental differences within a species of lycaenid regarding the association with ants have not been reported before. It can be concluded that, in *P. idas*, a large amount of biodiversity involves variation at the population level. Therefore, it is important for the preservation of genetic diversity to take this intraspecific variation into account in practical conservation management. The critically endangered population of the Upper Rhine valley constitutes a highly important conservation unit.

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References

Bähring A, Fichtner A, Ibe K, Schütze G, Temperton VM, von Oheimb G, Härdtle W (2017) Ecosystem functions as indicators for heathland responses to nitrogen fertilisation. Ecological Indicators 72: 185–193. https://doi.org/10.1016/j.ecolind.2016.08.013

Bink FA (1992) Ecologische Atlas van de Dagvlinders van Noordwest-Europa. Schuyt & Co., Haarlem, 512 pp.

Blatrix R, Galkowski C, Lebas C, Wegnez P (2013) Fourmis de France, de Belgique et du Luxembourg. Delachaux et Niestlé, Paris, 288 pp.

Bolz R (1998) Die Schmetterlingsfauna (Lepidoptera) der „Lockersandgebiete" in den Reichswäldern zu Nürnberg (Sebalder und Lorenzer Reichswald). Natur und Mensch 1997: 33–48. https://www.zobodat.at/pdf/Natur-und-Mensch_1997_0033-0048.pdf

Bolz R, Bräu M (2013) Idas-Bläuling. *Plebejus idas* (Linnaeus, 1761). In: Bräu M, Bolz R, Kolbeck H, Nunner A, Voith J, Wolf W (Eds) Tagfalter in Bayern. Ulmer, Stuttgart, 322–325.

Clarke HE (2022) A provisional checklist of European butterfly larval foodplants. Nota Lepidopterologica 45: 139–167. https://doi.org/10.3897/nl.45.72017

Dardenne B, Démares M, Guérard P, Hazet G, Lepertel N, Quinette J-P, Radigue F (2008) Papillons de Normandie et des îles Anglo-Normandes. Atlas des Rhopalocères et des Zygènes. Agence régionale de l'environnement de Haute-Normandie, Rouen, 200 pp.

Eastwood R, Fraser AM (1999) Associations between lycaenid butterflies and ants in Australia. Australian Journal of Ecology 24: 503–537. https://doi.org/10.1046/j.1440-169x.1999.01000.x

Eastwood R, Braby MF, Lohman DJ, King A (2008) New ant-lycaenid associations and biological data for some Australian butterflies (Lepidoptera: Lycaenidae). Australian Entomologist 35: 47–56. https://ia601409.us.archive.org/27/items/biostor-274314/biostor-274314.pdf

Ebert G, Rennwald E (1991) Die Schmetterlinge Baden-Württembergs. Band 2. Tagfalter II. Ulmer, Stuttgart, 536 pp.

Fiedler K (1991) Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). Bonner Zoologische Monographien 31: 1–210. https://www.academia.edu/18063234/Systematic_evolutionary_and_ecological_implications_of_myrmecophily_within_the_Lycaenidae_Insecta_Lepidoptera_Papilionoidea_

Fiedler K (1998) Lycaenid-ant interactions of the *Maculinea* type: tracing their historical roots in a comparative frame-work. Journal of Insect Conservation 2: 3–14. https://doi.org/10.1023/A:1009618721239

Fiedler K (2006) Ant-associates of Palearctic lycaenid butterfly larvae (Hymenoptera: Formicidae; Lepidoptera: Lycaenidae) – a review. Myrmekologische Nachrichten 9: 77–87. https://doi.org/10.25849/myrmecol.news_009:077

Fiedler K (2021) The ant associates of Lycaenidae butterfly caterpillars – revisited. Nota Lepidopterologica 44: 159–174. https://doi.org/10.3897/nl.44.68993

Fiedler K, Saam C (1995) Ants benefit from facultatively myrmecophilous Lycaenidae caterpillars: evidence from a survival study. Oecologia 104: 316–322. https://doi.org/10.1007/BF00328367

Fraser DJ, Bernatchez L (2001) Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Molecular Ecology 10: 2741–2752. https://doi.org/10.1046/j.0962-1083.2001.01411.x

Galkowski C (2024) *Formica fuscocinerea*, *Formica selysi* in AntArea – étude, identification, répartition, localisation des fourmis françaises métropolitaines [determinations of ant samples]. http://antarea.fr/fourmi/?repartition/repertition-especes.html [accessed 16.12.2024]

Gelbrecht J, Clemens F, Kretschmer H, Landeck I, Reinhardt R, Richert A, Schmitz O, Rämisch F (2016) Die Tagfalter von Brandenburg und Berlin (Lepidoptera: Rhopalocera und Hesperiidae). Naturschutz und Landschaftspflege in Brandenburg 25 (3,4): 1–326. https://lfu.brandenburg.de/sixcms/media.php/9/Heft%20N%26L_3-4_2016_inhalt.pdf

Gourvil P-Y, Sannier M (2022) Atlas des Papillons de jour d'Aquitaine. Biotope Éditions, Mèze & Muséum national d'Histoire naturelle, Paris, 464 pp.

Güsten R, Sanetra M, Trusch R (2019) Bläulinge (Lepidoptera: Lycaenidae) im Einzugsgebiet von Jagst und Kocher – Verbreitung, Ökologie und Vorschläge zu Schutzmaßnahmen. Carolinea 77: 93–143. https://www.smnk.de/uploads/tx_psbpublication/07_C77_Guesten_et.al.pdf

Haag M, Rennwald E, Schulte T (2007) Idas-Bläuling – *Plebejus idas* (Linnaeus, 1761). In: Schulte T, Eller O, Niehuis M, Rennwald E (Eds) Die Tagfalter der Pfalz, Band 1. Fauna und Flora in Rheinland-Pfalz, Beiheft 37. Gesellschaft für Naturschutz und Ornithologie Rheinland-Pfalz e.V., Landau, 350–356.

Henriksen HJ, Kreutzer IB (1982) The butterflies of Scandinavia in Nature. Skandinavisk Bogforlag, Odense, 215 pp. https://doi.org/10.1163/9789004631694

Hill GM, Trager MD, Lucky A, Daniels JC (2022): Protective benefits of tending ants to a critically endangered butterfly. Journal of Insect Science 22(6): 9. [10 pp.] https://doi.org/10.1093/jisesa/ieac068

Hölldobler B, Kwapich CL (2022) The Guests of Ants: How Myrmecophiles Interact with Their Hosts. The Belknap Press of Harvard University Press, Cambridge (Mass.) & London, 559 pp. https://doi.org/10.2307/j.ctv2n4w5m5

Jutzeler D (1989) Weibchen der Bläulingsart *Lycaeides idas* L. riechen ihre Wirtsameisen (Lepidoptera: Lycaenidae). Mitteilungen der Schweizer Entomologischen Gesellschaft Basel 39(3): 95–118. https://www.e-periodica.ch/digbib/view?pid=enh-003%3A1989%3A39%3A%3A102#102

Jutzeler D (1990) Weibchen von *Lycaeides idas* (Linnaeus, 1761) riechen ihre Wirtsameisen, Nachträge aus den Jahren 1989 und 1990 (Lepidoptera: Lycaenidae). Mitteilungen der Schweizer Entomologischen Gesellschaft Basel 40(1/2): 66–71. https://www.e-periodica.ch/digbib/view?pid=enh-003%3A1989%3A39%3A%3A102#102

Jutzeler D, Leigheb G (2004) Évaluation du statut taxinomique des populations côtières sardes de *Lycaeides bellieri* Oberthür (1910) se fondant sur du matériel d'élevage provenant de l'île de La Maddalena, Sardaigne du Nord (Lepidoptera: Lycaenidae). Linneana Belgica 19(6): 285–290. http://www.filming-varwild.com/articles/fr/david-jutzeler/84-2004-jutzeler-et-al-bellieri.pdf

Jutzeler D, Leigheb G, Manil L, Villa R, Volpe C (2003) Deux espèces de Lycènes négligées de l'espace tyrrhénien: *Lycaeides bellieri* Oberthür (1910) de Sardaigne et de Corse et *Lycaeides villai* sp. n., de l'île d'Elbe (Lepidoptera: Lycaenidae). Linneana Belgica 19(2): 65–80. http://www.filming-varwild.com/articles/fr/david-jutzeler/79-2003-jutzeler-et-al-bellieri-villai.pdf

Kolev Z (2005) Notes on the distribution and ecology of Balkan populations of the *Plebeius idas* – group (Lepidoptera: Lycaenidae). Phegea 33(1): 13–22. http://www.phegea.org/Phegea/2005/Phegea33-1_13-22.pdf

Kolligs D (2021) Die Schmetterlinge Schleswig-Holsteins – Checkliste aller Arten und Rote Liste der Großschmetterlinge [2 vol.]. 3. Fassung. Landesamt für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein, Flintbek, 124 + 123. https://umweltanwendungen.schleswig-holstein.de/Bestellsysteme/pdf/schmetterlinge/rl_schmetterlingebd1_2022.pdf, https://umweltanwendungen.schleswig-holstein.de/Bestellsysteme/pdf/schmetterlinge/rl_schmetterlingebd2_2022.pdf

Lafranchis T (2004) Butterflies of Europe. Diatheo, Paris, 350 pp. https://drive.google.com/file/d/14JOzgSNkntq-WCu5we-aqnTzLcdAyr2_/view

Lafranchis T, Jutzeler D, Guillosson J-Y, Kan P, Kan B (2015) La Vie des Papillons. Ecologie, Biologie et Comportement des Rhopalocères de France. Diatheo, Paris, 751 pp. https://drive.google.com/file/d/1PrK-W2oVCGBibYBXEGbF5ia_9LdxlCcLt/view

Lucek K, Blattner L, Cornet C, Chittaro Y, Erhardt A, Jaun A, Jost B, Winiger N, Wymann H-P, Dušej G (2024) Towards a genomic resolution of the *Phengaris alcon* species complex. Conservation Genetics 25: 823–834. https://doi.org/10.1007/s10592-024-01605-x

Maillard D (2014) Synthèse des connaissances relatives aux deux espèces *Plebejus argus* et *Plebejus idas* en Bretagne. Masters thesis, Brest & Rouen, France; Bretagne Vivante & University of Rouen, 70 pp. https://side.developpement-durable.gouv.fr/Default/doc/SYRACUSE/342437/synthese-des-connaissances-relatives-aux-deux-especes-plebejus-argus-et-plebejus-idas-en-bretagne?_lg=fr-FR

Maillard D (2017) *Plebejus idas* (Linnaeus, 1761). Azuré du Genêt. Glazig ar balan. In: Buord M, David J, Garrin M, Iliou B, Jouannic J, Pasco P-Y, Wiza S (Coords) Atlas des Papillons Diurnes de Bretagne. Locus Solus, Lopérec, 204–205.

Malicky H (1961) Über die Ökologie von *Lycaeides idas* L., insbesondere über seine Symbiose mit Ameisen. Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen 13: 33–49.

Miethke M (2011) *Plebejus idas* in Lepiforum e.V. (2024) Bestimmung von Schmetterlingen und ihren Präimaginalstadien [photograph of oviposition on *Calluna vulgaris*]. https://lepiforum.de/lepiwiki_vgl.pl?action=browse&id=Plebejus_Idas&revision=80 [accessed 16.12.2024]

Muñoz Sariot MG (2011) Biología y ecología de los Licénidos Españoles. M. G. Muñoz Sariot, Granada, 383 pp.

Niemeyer M, Niemeyer T, Fottner S, Härdtle W, Mohamed A (2007) Impact of sod-cutting and choppering on nutrient budgets of dry heathlands. Biological Conservation 134: 344–353. https://doi.org/10.1016/j.biocon.2006.07.013

Pedley SM, Franco AMA, Pankhurst T, Dolman PM (2013) Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. Biological Conservation 160: 173–182. https://doi.org/10.1016/j.biocon.2013.01.006

Perrein C (2012) Biohistoire des Papillons. Diversité et conservation des lépidoptères rhopalocères en Loire-Atlantique et en Vendée. Presses Universitaires, Rennes, 622 pp. https://side.developpement-durable.gouv.fr/PDLO/doc/SYRACUSE/222873/biohistoire-des-papillons-diversite-et-conservation-des-lepidopteres-rhopaloceres-en-loire-atlantique

Pfeuffer E (1998) Zur Myrmekophilie des Idas-Bläulings (*Lycaeides idas* L.). Beobachtungen an den Dämmen der Lechstaustufen im Unteren Lechtal. Berichte des naturwissenschaftlichen Vereins für Schwaben 102: 41–56. https://www.zobodat.at/pdf/Ber-Naturwiss-Ver-fuer-Schwaben_102_0041-0056.pdf

Pfeuffer E (2003) Der Idas-Bläuling (*Plebejus idas* Linnaeus 1771) am Lech. Berichte des naturwissenschaftlichen Vereins für Schwaben 107: 64–81. https://www.zobodat.at/pdf/Ber-Naturwiss-Ver-fuer-Schwaben_107_0064-0081.pdf

Pfeuffer E (2005) Nachtrag zu: Der Idas-Bläuling (*Plebejus idas* Linnaeus 1771) am Lech. Berichte des naturwissenschaftlichen Vereins für Schwaben 109: 108–112. https://www.zobodat.at/pdf/Ber-Naturwiss-Ver-fuer-Schwaben_109_0108-0112.pdf

Phoenix GK, Emmett BA, Britton AJ, Caporn SJM, Dise NB, Helliwell R, Jones L, Leake JR, Leith ID, Sheppard LJ, Sowerby A, Pilkington MG, Rowe EC, Ashmore MR, Power SA (2012) Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. Global Change Biology 18: 1197–1215. https://doi.org/10.1111/j.1365-2486.2011.02590.x

Pierce NE, Dankowicz E (2022a) The Natural History of Caterpillar-Ant Associations. In: Marquis RJ, Koptur S (Eds) Caterpillars in the Middle. Springer, Cham, 319–391. https://doi.org/10.1007/978-3-030-86688-4_11

Pierce NE, Dankowicz E (2022b) Behavioral, ecological and evolutionary mechanisms underlying caterpillar-ant symbioses. Current Opinion in Insect Science 52: 100898. [9 pp] https://doi.org/10.1016/j.cois.2022.100898

Pierce NE, Easteal S (1986) The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*. Journal of Animal Ecology 55: 451–462. https://doi.org/10.2307/4730

Pierce NE, Elgar MA (1985) The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. Behavioral Ecology and Sociobiology 16: 209–222. https://doi.org/10.1007/BF00310983

Pierce NE, Nash DR (1999) The Imperial Blue: *Jalmenus evagoras* (Lycaenidae). In: Kitching RL, Scheermeyer E, Jones RE, Pierce NE (Eds) Biology of Australian Butterflies. Monographs on Australian Lepidoptera, Vol. 6. CSIRO Publishing, Collingwood, 277–313. https://books.google.de/books/about/Biology_of_Australian_Butterflies.html?id=cTFychx78QIC&redir_esc=y

Pierce NE, Kitching RL, Buckley RC, Taylor MFJ, Benbow KF (1987) The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. Behavioural Ecology and Sociobiology 21: 237–248. https://doi.org/10.1007/BF00292505

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology 47: 733–771. https://doi.org/10.1146/annurev.ento.47.091201.145257

Pontin AJ (1990) *Plebejus argus* L. (Lep., Lycaenidae) pupae in nests of *Lasius niger* (L.) (Hym., Formicidae). Entomologists' Monthly Magazine 126: 73.

Powell H (1917) Observations relatives à *Lycaena armoricana*. Études de Lépidoptérologie Comparée 14: 420–460, plate CDLXXXI[bis], b/w plates unnumbered & A–F. http://www.biodiversitylibrary.org/item/40409#page/622/mode/1up, http://www.biodiversitylibrary.org/item/40409#page/717/mode/1up, http://www.biodiversitylibrary.org/item/40409#page/719/mode/1up

Reinhardt R, Bolz R (2012) Rote Liste und Gesamtartenliste der Tagfalter (Rhopalocera) (Lepidoptera: Papilionoidea et Hesperioidea) Deutschlands. In: Binot-Hafke M, Balzer S, Becker N, Gruttke H, Haupt H, Hofbauer N, Ludwig G, Matzke-Hajek G, Strauch M (Eds) Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 3: Wirbellose Tiere (Teil 1). Naturschutz und Biologische Vielfalt 70 (3). Bundesamt für Naturschutz, Bonn-Bad Godesberg, 167–194.

Reinhardt R, Sbieschne H, Settele J, Fischer U, Fiedler G (2007) Tagfalter von Sachsen. In: Klausnitzer B, Reinhardt R (Eds) Beiträge zur Insektenfauna Sachsens. Band 6. Entomologische Nachrichten und Berichte, Beiheft 11. Entomofaunistische Gesellschaft e.V., Dresden, 696 + 48 pp.

Romiguier J, Rolland J, Morandin C, Keller L (2018) Phylogenomics of palearctic *Formica* species suggests a single origin of temporary parasitism and gives insights to the evolutionary pathway toward slavemaking behaviour. BMC Evolutionary Biology 18 (40): 1–8. https://doi.org/10.1186/s12862-018-1159-4

Schweizerischer Bund für Naturschutz (1987) Tagfalter und ihre Lebensräume. Band 1. Pro Natura, Basel, 516 pp.

Schwibinger M, Bräu M (2001): Die Tagfalterfauna des Naturraums Münchener Ebene gestern und heute (Insecta, Lepidoptera, Rhopalocera). Nachrichtenblatt der Bayerischen Entomologen 50: 152–174. https://www.zobodat.at/pdf/NachBlBayEnt_050_0152-0176.pdf

Seifert B (2018) The Ants of Central and North Europe. lutra Verlags- und Vertriebsgesellschaft, Tauer, 408 pp.

Singer MC, McBride CS (2012) Geographic mosaics of species' association: a definition and an example driven by plant–insect phenological synchrony. Ecology 93: 2658–2673. https://doi.org/10.1890/11-2078.1

Strätling R (2009) *Plebejus idas* in Lepiforum e.V. (2024) Bestimmung von Schmetterlingen und ihren Präimaginalstadien [photograph of *Cytisus scoparius* as host plant]. https://lepiforum.de/lepiwiki_vgl.pl?action=browse&id=Plebejus_Idas&revision=80 [accessed 16.12.2024]

Tartally A, Thomas JA, Anton C, Balletto E, Barbero F, Bonelli S, Bräu M, Casacci LP, Csősz S, Czekes Z, Dolek M, Dziekańska I, Elmes G, Fürst MA, Glinka U, Hochberg ME, Höttinger H, Hula V, Maes D, Munguira ML, Musche M, Nielsen PS, Nowicki P, Oliveira P, Peregovits P, Ritter S, Schlick-Steiner BC, Settele J, Sielezniew M, Simcox DJ, Stankiewicz AM, Steiner F, Švitra G, Ugelvig LV, Van Dyck H, Varga Z, Witek M, Woyciechowski M, Wynhoff I, Nash DR (2019) Patterns of host use by brood parasitic *Maculinea* butterflies across Europe. Philosophical Transactions of the Royal Society B: Biological Sciences 374: 20180202. [17 pp.] https://doi.org/10.1098/rstb.2018.0202

Thomann H (1901) Schmetterlinge und Ameisen. Beobachtungen über eine Symbiose zwischen *Lycaena argus* L. und *Formica cinerea* Mayr. Jahresbericht der Naturforschenden Gesellschaft Graubündens 44: 1–40. [+plate] http://doi.org/10.5169/seals-594740

Thomas CD, Glen SWT, Lewis OT, Hill JK, Blakeley DS (1999) Population differentiation and conservation of endemic races: the butterfly, *Plebejus argus*. Animal Conservation 2: 15–21. https://doi.org/10.1111/j.1469-1795.1999.tb00044.x

Thompson JN (2005) The Geographic Mosaic of Coevolution. University of Chicago Press, Chicago, 442 pp. https://doi.org/10.7208/chicago/9780226118697.001.0001

Thompson JN, Schwind C, Guimarães Jr. PR, Friberg M (2013) Diversification through multitrait evolution in a coevolving interaction. Proceedings of the National Academy of Sciences of the United States of America 110: 11487–11492. https://doi.org/10.1073/pnas.1307451110

Trager MD, Thom MD, Daniels JC (2013) Ant-Related Oviposition and Larval Performance in a Myrmecophilous Lycaenid. International Journal of Ecology 2013: 152139. [9 pp.] https://doi.org/10.1155/2013/152139

Trusch R, Steiner A, Nuß M, Bauer F (2024) Schmetterlinge Deutschlands [distribution map]. https://www.schmetterlinge-d.de/Lepi/EvidenceMap.aspx?Id=441036 [accessed 16.12.2024]

Tshikolovets VV (2011) Butterflies of Europe and the Mediterranean area. Tshikolovets Publications, Kyiv, 544 pp.

Ulrich R (2004) Habitatselektion des Idasbläulings (*Plebeius idas* Linnaeus, 1761) mit besonderer Berücksichtigung des Eiablageverhaltens, dargestellt an einer Population auf einem Kalkhalbtrockenrasen im südöstlichen Saarland (Lepidoptera: Lycaenidae). Nachrichten des Entomologischen Vereins Apollo N.F. 25 (4): 175–180. https://www.zobodat.at/pdf/NEVA_25_0175-0180.pdf

Walmsley DC, Delory BM, Alonso I, Temperton VM, Härdtle W (2021) Ensuring the Long-Term Provision of Heathland Ecosystem Services – The Importance of a Functional Perspective in Management Decision Frameworks. Frontiers in Ecology and Evolution 9: 791364. [15 pp.] https://doi.org/10.3389/fevo.2021.791364

Ward PS, Blaimer BB, Fisher BL (2016) A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. Zootaxa 4072: 343–357. https://doi.org/10.11646/zootaxa.4072.3.4

Weidemann HJ (1995) Tagfalter beobachten, bestimmen (2nd edn.). Naturbuch Verlag, Augsburg, 659 pp.